

Effect of Predation and Environmental Patchiness on the Body Size of a Tropical Pulmonate Limpet

BY

BRUCE A. MENGE¹

Department of Zoology, University of Washington, Seattle, Washington 98105

(1 Plate; 3 Text figures)

INTRODUCTION

IN RECENT YEARS, a rapidly expanding body of knowledge on predation and its effects has focused attention on its importance in structuring communities (*e. g.*, PAINE, 1966, 1969; DAYTON, 1971; HALL, COOPER, & WERNER, 1970). Particular emphasis has been placed on the impact of selective prey consumption, a trait previously recognized by zoologists as nearly universal among animals. A parameter of major significance in prey selection is prey size (BROOKS & DODSON, 1965; BROOKS, 1968; DODSON, 1970; WELLS, 1970) and the work of HALL, COOPER, & WERNER (*op. cit.*) suggests that the structure of many temperate pond communities largely revolves around size-selective predation and its effects. However, our knowledge of the functioning of tropical communities is relatively poor; hence, the generality of studies based on temperate communities is not entirely clear.

In this note I suggest that the dispersion and size frequency patterns of the tropical pulmonate limpet, *Siphonaria normalis* Gould, 1846 largely result from size-selective predation by a carnivorous gastropod, *Thais armigera* (Link, 1807).

STUDY AREAS

The study was carried out in August, 1970 on the seaward reef platforms of Eniwetok Island and Parry Island, two of about 40 islands on Eniwetok Atoll (latitude 11°21' N, longitude 161°21' E), Marshall Islands (Figure 1). The reef platform or bench is composed of a flat, homogeneous inner bench and an extremely hetero-

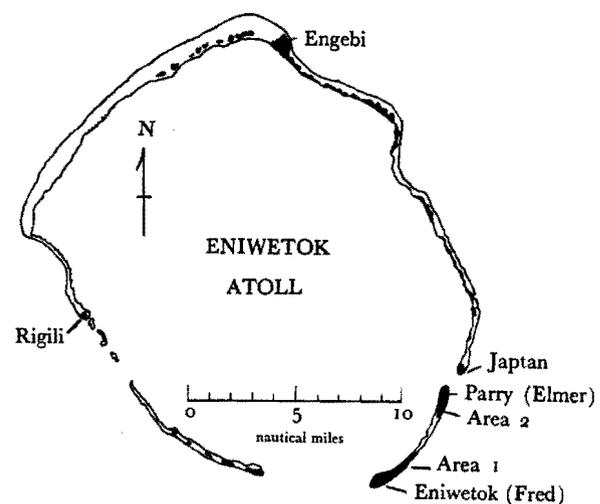


Figure 1

Map of Eniwetok Atoll, Marshall Islands. Areas 1 and 2 are the study areas on Eniwetok and Parry Islands, respectively. Prevailing winds are from the east-northeast. The black areas represent the islands, the outlined white areas represent the reef

geneous fringing algal ridge (see KOHN, 1967; TRACEY, CLOUD, & EMERY, 1955). Landward, the inner bench terminates abruptly against a steep beach of sand, shells and shell fragments of the gastropod genera *Conus*, *Drupa*, *Morula*, *Cerithium*, and *Cypraea* (Figure 2). The climate is tropical marine and prevailing conditions are warm temperate (daily maximum temperature is 30° C, minimum is 25.5° C), with high humidity, partly cloudy

¹ Present address: Department of Biology, University of Massachusetts, Boston, Massachusetts 02116

skies, moderate easterly tradewinds and occasional rain showers. The only notable seasonal change in weather is the usual occurrence of doldrums from June through October (U. S. Air Force, 1970).

Dominant macroinvertebrates on the reef include the gastropods *Thais armigera*, *Siphonaria normalis*, *Conus chaldeus* Röding, 1798, *C. ebraeus* Linnaeus, 1758, *Morula uva* (Röding, 1798), *Drupa morum* Röding, 1798, *Cypraea moneta* Linnaeus, 1758, *Cerithium* spp. and the hermit crabs *Calcinus* spp., *Diogenes* spp., and *Clibonarius* spp. In addition, individuals of the snails *Nerita plicata* Linnaeus, 1758 and *N. albiscillia* Linnaeus, 1758 occasionally wander onto the shoreward edge of the flat. Dominant type of algae on the inner bench were a non-calcareous red alga (?*Peyssonelia* sp.), a blue-green alga and encrusting melobesiod (coralline) algae; tufts of an unidentified filamentous brown alga and a red alga, *Martensia* sp., were locally abundant toward the seaward edge of the reef (personal observations; DAWSON, 1956; assistance in identification from J. Norris).

There were three major differences observed between the two reef platforms. First, the Parry Island reef platform is slightly higher in elevation than the Eniwetok Island reef. Associated with this is the difference in types of algae present; on Parry Island virtually 100% of the substratum was covered with encrusting algae while on Eniwetok Island encrusting algae occurred in patches scattered in a "lawn" of algal "turf". Second, the gastropod *Thais armigera* is very rare at Eniwetok Island and locally abundant on Parry Island. Within the *Thais*-dense area (a 200 m stretch of shore) densities of 0.72/m² were recorded (a total of 316 m² were sampled); beyond the dense area, abundance of *Thais* was similar to that observed on Eniwetok Island, where a total of about 7 individuals were observed on a 2 km stretch of the reef. Although some *Thais* were certainly missed, it is clear that this gastropod was quite scarce (for unknown reasons) on Eniwetok Island. Third, the distribution of pulmonate limpets

(size range: 1 to 12 mm), *Siphonaria normalis*, is characteristically patchy on Eniwetok Island, whereas on Parry Island they are distributed relatively evenly over the whole flat. The patchiness of *Siphonaria* on Eniwetok Island seems to result from the patchy distribution of a suitable substratum (*i. e.*, one covered only with encrusting algae, in this case coralline algae); in turn this may have resulted from the difference in elevation between the two reefs.

PATTERNS OF DISTRIBUTION AND ABUNDANCE OF *Siphonaria normalis*

Mean densities of limpets within the *Siphonaria*-favorable patches on Eniwetok Island are somewhat higher than those on Parry Island (Table 1). Further, local differences in size-frequency exist at the latter area but not at the former. A comparison between the density and size of the limpets in the pools with encrusting coralline algae covering the bottom and those in pools with a very slippery *Peyssonelia*-like alga, reveals that coralline algae pools have many small *Siphonaria* and non-coralline pools contain a few large *Siphonaria*. Moreover, in proceeding from coralline algae pools to pool edges to emergent substratum between the pools ("ridges") on Parry Island, *Siphonaria* density decreases while mean individual size increases (Table 1, Figure 3). This pattern does not occur on Eniwetok Island, where both density and limpet size are rather uniform within the *Siphonaria* patches (Table 1).

Observations of these limpets returning to home scars on Eniwetok Island (Figure 4) confirms Cook's experiments (1969) on the homing behavior of this limpet. Local size or abundance patterns should therefore be affected little by migration. In the next section, I suggest that the primary cause of the patchy size-frequency distribution of *Siphonaria* is size-selective predation by *Thais* coupled with environmental heterogeneity.

Explanation of Figures 2 to 4

Figure 2: View of area 2 looking southwest towards Eniwetok Island (just visible in the center-left of the photograph). Note the shallow pools and the "ridges" between them. The cylindrical object in the right foreground is about 2 feet long and protects 20 to 30 *Thais armigera*

Figure 3: Comparison between the size of *Siphonaria* in shallow tide pools (right) to that on the emergent substratum between the pools or "ridges" (left) at Parry Island (area 2). The dark color of the "ridge" substratum is caused by blue-green algae

Figure 4: Close-up photograph of *Siphonaria in situ* and their "scars" or homing sites, several of which are vacant



Figure 2

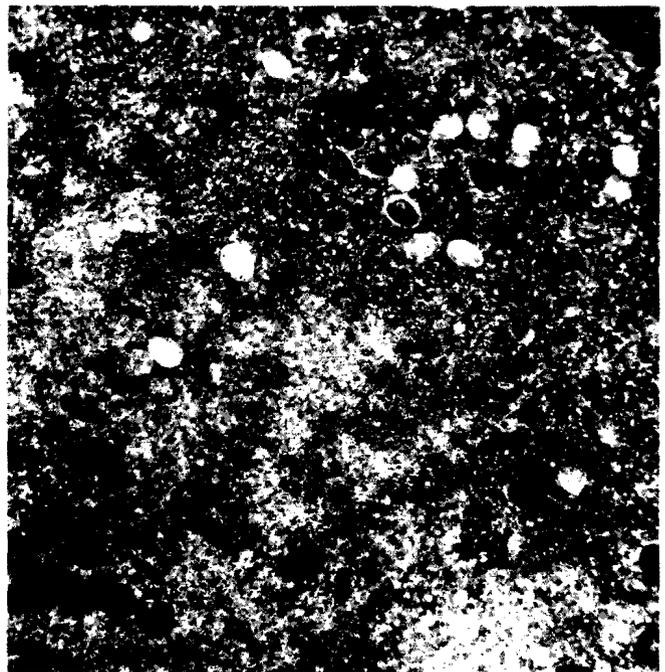


Figure 4

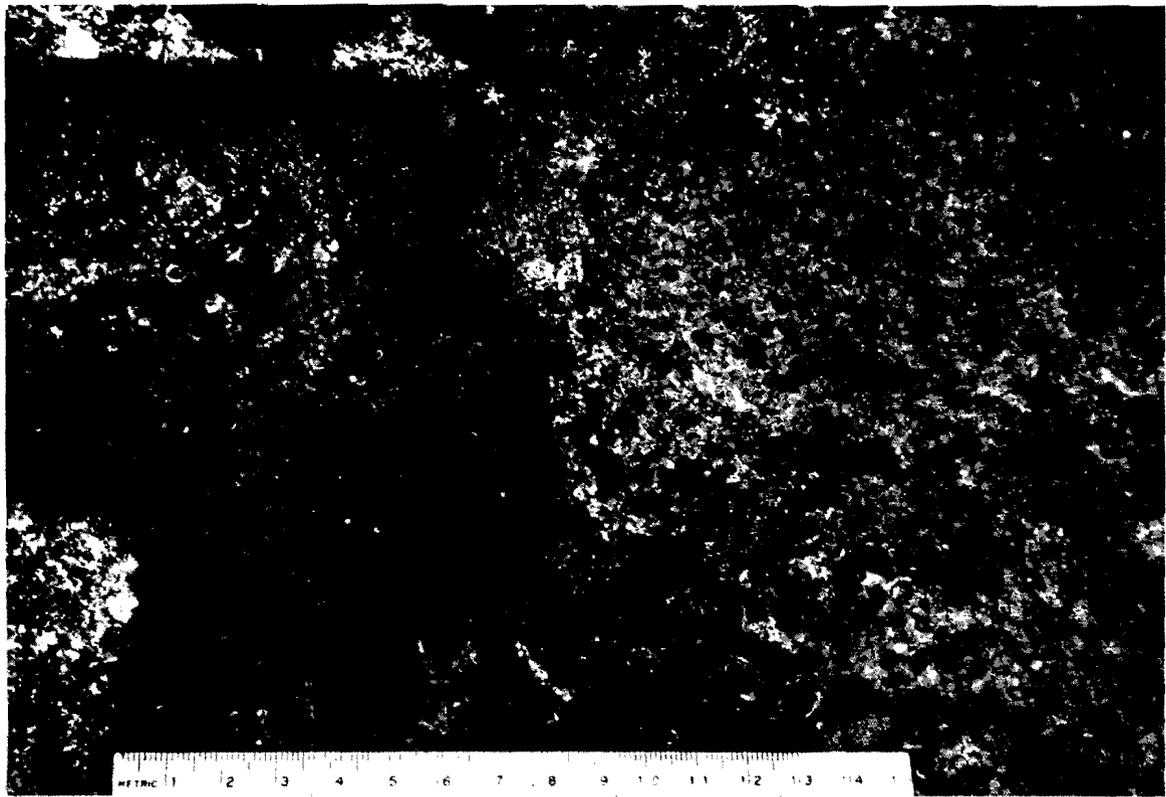


Figure 3

Table 1

Density of *Siphonaria normalis* at Two Areas on Eniwetok Atoll²

A. PARRY ISLAND

Substratum Characteristics	Density (no./m ²) ± 95% confidence interval	N	No. of quadrats where size of <i>Siphonaria</i> is predominantly ³		
			Large	Medium	Small
Encrusting non-calcareous algae, pool	150 ± 106	20	6	3	1
Encrusting coralline algae and detritus, pool	6150 ± 1329	19	0	5	12
Edge of pool	3361 ± 748	34	3	17	3
Dry substratum	438 ± 293	15	8	0	0
Average	2648 ± 620	81			

B. ENIWETOK ISLAND⁴

Substr. characteristics	Density (no./m ²) ± 95% confidence interval	N
Encrusting coralline algae and detritus, damp	3473 ± 360	7

² Size of haphazardly placed quadrats: Parry Island, 100 cm²; Eniwetok Island, 400 cm²

³ Totals do not equal N because some quadrats had no limpets in them

⁴ Nearly all *Siphonaria* on Eniwetok Island were "medium" in size

FORAGING HABITS OF *Thais*

The majority of observations on *Thais armigera* were made on Parry Island. Capture of prey by *Thais* is accomplished by placing the head and anterior end of the foot over the relatively flat limpet and turning it over; once the limpet is positioned properly, *Thais* rasps the flesh out with its radula. (The mode of prey detection is unknown.) Feeding observations are made by turning over a *Thais*, examining it for prey, and measuring predator and prey length in millimeters.

Table 2 shows the percent of *Thais* feeding during a variety of tide and light conditions (excluding night high tides only). Feeding frequency was fairly constant during the interval of study, averaging 18.5% of the population over all tide and light combinations. The amount of variation in feeding and reproduction of *Thais* over longer intervals is unknown.

Table 2

Percent of *Thais armigera* Feeding at the Parry Island Study Area, August 1970

Date	Light and Tide	Number Observed	Number Feeding	% Feeding
8/VIII/70	Day Low Tide	104	21	20.2
13/VIII/70	Day High Tide	234	32	13.7
14/VIII/70	Day High Tide	91	18	19.8
18/VIII/70	Night Low Tide	150	27	18.0
23/VIII/70	Day Low Tide	130	27	20.8
Total		709	125	18.5

In August, 1970, the diet of *Thais* was nearly monospecific, with the *Siphonaria* accounting for 99.2% (131) of the observations and the herbivorous snail, *Nerita albicillia*, accounting for the remaining 0.8% (1 individual). Other molluscan prey are rare in the environment, but might be eaten by *Thais* if encountered.

DISPERSION PATTERN OF *Thais*

The dispersion pattern of *Thais* and the percent of the population feeding suggest that relatively more of its time is spent feeding in tide pools. The direction of deviation of the observed distribution of *Thais* from a Poisson (random) pattern of distribution indicates that at low tide this snail is contagiously distributed on the reef flat (*i.e.*, there are more 1 m² quadrats with 3 and 4 *Thais* per quadrat and fewer with 1 and 2 than expected by chance alone; see Figure 5). Although the cause of this contagion is not known, two observations suggest that desiccation plays a major role in patterns of *Thais* dispersion. First, *Thais* microdistribution is strongly correlated with that of the small, shallow pools scattered over the reef (Table 3) at low tide; 83.2% of 113 *Thais* were observed in these pools, with a total of 92.1% observed on "wet" substratum. Subjective estimates of the percent of the substratum covered by tide pools (in 80 1-m² quadrats) indicate that 65.4 ± 4.0% of the total Parry Island area is underwater at low tide. Thus *Thais* appears to be in tide pools more

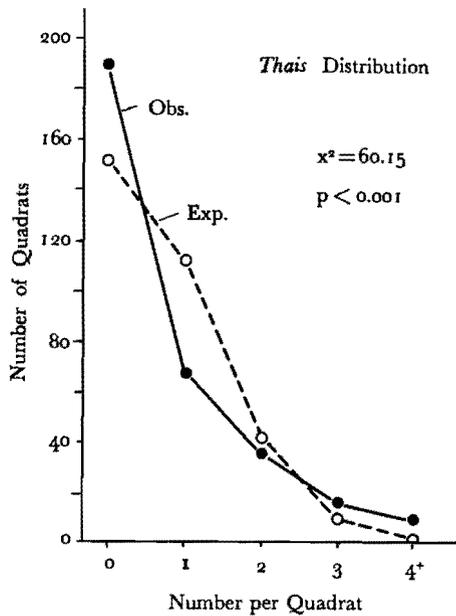


Figure 5

Comparison between the observed number of quadrats containing 0, 1, 2, 3, and 4 or more *Thais* and the number expected. Chi square shows that the observed curve is significantly different from the expected (Poisson) distribution (*i. e.*, the *Thais* are non-randomly distributed)

Table 3

Thais armigera Distribution According to Wetness of Substratum

Substratum type	Number of <i>Thais</i>	% of total
Wet - Tide pools	94	83.2
- Depressions	8	7.1
- "Ridges"	2	1.8
Wet Total	104	92.1
Dry - Depressions	6	5.3
- "Ridges"	2	1.8
- Top of Rock	1	0.9
Dry Total	9	8.0
Grand Total	113	100.1

frequently than expected by chance, suggesting that there is a preference for wet habitats. Second, observations of the distribution of *Thais* under and around a cylindrical piece of scrap metal located within the *Thais* patch on

Parry Island (shown in Figure 2) show that about 20 - 30 *Thais* are located around and under the metal object. A zone of about 6m radius around this object contained virtually no *Thais*, and beyond this zone densities increased to the normal 0.7/m². Since *Siphonaria* are distributed over both wet and dry substratum (Table 1) and pools afford no obvious shelter to *Thais* from potential predators, the most probable factor responsible for this apparent preference for wetness or cool, damp crevices is desiccation or some related physical factor. This preference for tidepools at low tide means that a relatively greater proportion of this predator's time budget will be spent in such microhabitats. Hence, the *Siphonaria* in pools would probably be subject to more intense predation than those outside the tidepools.

In view of these data, several hypotheses can be proposed to explain the observed size-frequency pattern of *Siphonaria* (Figure 4, Table 1). First, size-selective predation by *Thais* (which spends relatively more of its time in pools) may cause the observed pattern. Second, *Siphonaria* may settle preferentially in the pools and gradually migrate to the ridges. Third, *Siphonaria* may settle uniformly over the reef flat, but perhaps because of desiccation, survive better in the pools than on the ridges. In this case, the few survivors on the ridges would have more food available (assuming little difference in availability of food for the limpets existed between pools and ridges) and would grow large because of their reduced density. Fourth, considering that in certain tidepools (*i. e.*, those with *Peyssonelia* as the dominant encrusting algae; Table 1) limpet density and size pattern were similar to those on the ridges, a cause of the patterns observed may reside in some subtle effect of the substratum or food on *Siphonaria*. Finally, a hypothesis combining elements of the above three hypotheses is that *Thais* may crawl to the ridges for food and return to the pools to consume any prey captured.

The data in Figure 6, which compare the size frequencies of *Siphonaria* available in the pools and on the "ridges" to the size of limpets eaten by *Thais*, support the first hypothesis by showing that this snail selects the largest prey available. The observation that the *Siphonaria* size pattern noted above does not occur on Eniwetok Island, where *Thais* is virtually absent provides further support for this hypothesis. Because nothing was known about *Siphonaria* reproduction and time was limiting, it was not possible to test the other hypotheses. However, the homing response of *Siphonaria* (Cook, 1969; see above) mitigates against the second hypothesis and, since in most cases, *Thais* were observed to consume prey on or near the site of capture, the last hypothesis is viewed as unlikely as

well. The third and fourth hypotheses remain reasonable possibilities.

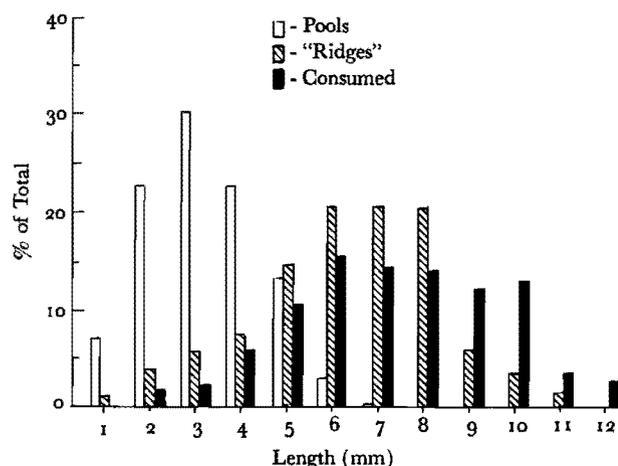


Figure 6

Size frequency histogram comparing the sizes of *Siphonaria* in pools and on "ridges" to the size eaten by *Thais armigera*

DISCUSSION

Although limited in their temporal extent, the data presented above provide a compelling argument that the absence of large *Siphonaria* from tidepools is largely caused by size-selective predation by *Thais armigera*. As yet unanswered are the effects of desiccation, food preference, and palatability on this size-frequency pattern.

Despite the fact that ecologists have long been aware of the importance of increasing our knowledge of tropical ecosystems, particularly with respect to understanding the causes of patterns of species diversity, we remain essentially ignorant of the relative effects of predation and competition in the tropics. I believe that unequivocal statements regarding the causes of patterns of distribution, size, abundance, and thus the causes of differences in species diversity, will ultimately be obtained by the proven and powerful manipulative-natural historical type of research (e.g., CONNELL, 1961a, 1961b, 1970; PAINE, 1966, 1969, 1971; DAYTON, 1971; HALL, COOPER, & WERNER, 1970; MENGE, 1972). Although the major value of this report is clearly heuristic, I feel this paper represents a small step toward the clarification of the role of invertebrate predators in the tropics.

ACKNOWLEDGMENTS

I thank Robert T. Paine, Alan J. Kohn, Paul K. Dayton, and Jane L. Menge for constructive criticisms of versions of the manuscript. Rick Vance provided field assistance and discussion of the research while it was in progress. Gastropod identifications were provided by Walter O. Cernohorsky, Curator of Molluscs, Auckland Institute and Museum, Auckland, New Zealand.

The research was carried out at the Eniwetok Marine Biological Laboratory and was supported by Atomic Energy Commission contract No. AT(29-2)-226 to EMBL. I thank Philip Helfrich, Director of EMBL, and his staff for their efforts in my behalf.

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